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ORIGINAL PAPER

An evaluation of the current extent and potential spread of Black Bass invasions in South Africa

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Abstract Black Bass, a collective name for members of the centrarchid genus *Micropterus*, are native to North America, but have been introduced globally to enhance recreational angling. This study assessed the distribution of *Micropterus salmoides*, *M. dolomieu* and *M. punctulatus* in South Africa using both formal (survey-based) and informal (tournament data and social media) information sources. Analysis of the distribution data showed habitat bias between the data sources. Survey data from formal information sources were dominated by locality records in riverine environments while those derived from informal information sources focused more on lacustrine habitats. Presence data were used to develop niche models to identify suitable areas for their establishment. The predicted distribution range of *M. salmoides* revealed a broad suitability over most of South Africa, however, the Cape Fold Ecoregion and all coastal regions were most suitable for the establishment for both *M. dolomieu* and *M. punctulatus*. Flow accumulation and precipitation of coldest quarter were the most important environmental variables associated with the presence of all Black Bass species in South Africa. In addition, anthropogenic disturbance such as

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agricultural activities were associated with the presence of both Smallmouth Bass and Spotted Bass. An extensive area-based invasion debt was observed for all *Micropterus* spp. The potential for further spread of Black Bass in South Africa is of ecological concern because of their impact on native biota.

Keywords *Micropterus* · Aquatic invasive species · Invasion debt · Fish distribution databases

Introduction

Freshwater ecosystems are threatened by multiple stressors which include habitat destruction and modification, overexploitation, pollution, and the introduction of non-native species (Bellard et al. 2016; Jackson et al. 2016; Venohr et al. 2018). The introduction of non-native fishes is considered one of the least reversible of these stressors (Simberloff 2003; Strayer 2010). Major conservation implications associated with non-native fish introductions are extinctions of native biota related to direct predation and competition, habitat modification, alteration of food webs and hybridisation with congeneric native species (Eby et al. 2006; Cucherousset and Olden 2011; Jackson et al. 2017). Most of the introduction and spread of non-native fishes are mediated by human activities (Leprieur et al. 2008; Ellender and Weyl 2014) and direct introductions for fisheries enhancements are the most important pathway for new invasions (Gozlan et al. 2010; Ellender and Weyl 2014; Venohr et al. 2018). As a result, considerable effort has gone into documenting non-native fish introductions (e.g. Welcomme 1988; Casal 2006; ISSG 2009; Ellender and Weyl 2014). Despite this, there is still a paucity of information on their subsequent establishment, spread and abundance which can often be attributed to the substantial cost of large-scale post-introduction assessments (Gillett et al. 2012; Bird et al. 2014; Hargrove et al. 2015).

Black Bass is the collective term for fishes of the genus *Micropterus* which are native to North America, east of the Rocky Mountains (Robbins and MacCrimmon 1974; Near et al. 2003) but have been introduced into areas outside their natural distribution range to enhance angling opportunities (Long et al. 2015; Weyl et al. 2017). Four species, Largemouth Bass *Micropterus salmoides* (Lacepède 1802), Florida Bass *M. floridanus* (Lesueur 1822), Smallmouth Bass *M. dolomieu* (Lacepède 1802) and Spotted Bass *M. punctulatus* (Rafinesque 1819) have been introduced, and now contribute to economically important recreational fisheries, outside of their native range in North America, Europe, Asia, South America and Africa (Jackson 2002; Takamura 2007; Hargrove et al. 2015; Long et al. 2015; Weyl and Cowley 2015).

In South Africa, Black Bass were specifically introduced to develop sport fisheries in areas that were too warm for Rainbow Trout *Oncorhynchus mykiss* (Walbaum 1792) and Brown Trout *Salmo trutta* Linnaeus 1758 (Ellender et al. 2014). Largemouth Bass were first imported in 1928 for use mainly in lentic environments, followed by Smallmouth Bass introduced in 1937 for introduction into rivers and Spotted Bass in 1939 for use in more turbid riverine environments (Ellender et al. 2014). Florida Bass were then introduced in 1980 to enhance Largemouth Bass fisheries because they attain larger sizes (Weyl et al. 2017). As Florida Bass are morphologically almost identical to, and hybridise with Largemouth Bass, it is currently not possible to distinguish between the two species without genetic verification (Weyl et al. 2017). It was, therefore, necessary to combine Largemouth Bass and Florida Bass to reduce identification bias, and Largemouth Bass, Florida Bass and their potential hybrids are hereafter referred to as Largemouth Bass.

Following their introduction, Black Bass were subsequently stocked via government supported stocking programs (until the early 1990s) and directly by anglers. While these introductions served the purpose of enhancing recreational fisheries, their subsequent invasions have also resulted in negative impacts on native biota (Ellender et al. 2014; Ellender and Weyl 2014) which include the extirpation of native fishes in Black Bass invaded habitats (e.g. Van Der Walt et al. 2016; Ellender et al. 2018). For example, in the Cape Fold Ecoregion (CFE) Black Bass species are implicated in the disappearance of several endemic cyprinid species and the anabantid *Sandelia capensis* (Cuvier 1829) (Shelton et al. 2008; Van Der Walt et al. 2016; Ellender et al. 2017). Similar impacts have been reported from Japan (Iguchi et al. 2004; Takamura 2007), the Iberian Peninsula in Europe (Godinho and Ferreira 2000) and other parts of southern Africa (Gratwicke and Marshall 2001).

The development of economically important fisheries around species that impact negatively on native ecosystems often results in conflicts between different stakeholders (e.g. Ellender et al. 2014; Zengeya et al. 2017) and their management is considered a "wicked problem" (Woodford et al. 2016). South Africa's legislated management response is to facilitate economic activities in invaded areas while restricting activities such as stock enhancements to prevent further spread (Woodford et al. 2017). As the invasion by non-native fishes is generally irreversible after they have established and impossible to eradicate without affecting the native biota (Simberloff 2003; Vitule et al. 2009; Cucherousset and Olden 2011), the most practical management strategy is to monitor and document their distribution and promote measures to limit their spread (Iguchi et al. 2004; Zengeya et al. 2013). As a result, understanding the current distribution; and estimating the potential for spread by using correlative methods (e.g. ecological niche modelling) that match occurrence data with environmental variables to identify suitable areas for establishment (Stockwell and Peterson 2002; Phillips and Dudík 2008; Elith et al. 2011) are vital for the effective implementation of the regulations.

In recent years there have been an increase in the development of algorithms to model ecological niches and species distributions. In this regard, species distribution models (SDM) are important as they provide knowledge on the global distributions and evolutionary patterns of biodiversity (Phillips and Dudík 2008). Species distribution models correlate species occurrence to the environmental characteristics (both continuous and categorical) of localities where the species occur (Elith et al. 2006). Among the available algorithms, MAXENT has performed well and is among the most widely used presence only modelling techniques (Elith et al. 2006, 2011).

For fishes in South Africa, formal sources of information on distributions include occurrence records held by provincial conservation authorities (e.g. CapeNature, Ezemvelo KwaZulu-Natal Wildlife), research institutions (e.g. South African Institute for Aquatic Biodiversity fish collections) and online repositories (e.g. Global Biodiversity Information Facility). A major limitation of such records is that they are often biased towards species and areas of interest to the organisation doing the collecting (e.g. non-native species were until recently often not curated in Museum collections) and thus do not reflect the full distributional range of many non-native species (Devictor et al. 2010; Tye et al. 2016). As a result, informal data (e.g. blogs, angler databases and social networks), are increasingly being used to complement formal distribution data (Forrester et al. 2015; Tye et al. 2016). Hargrove et al. (2015) for example, used angling tournament data to assess for the presence, establishment and stock status of Black Bass in southern African reservoirs and Gago et al. (2016) used informal online data sources to assess the spatial extent of spread of the European catfish, *Silurus glanis* Linnaeus 1758 in the Iberian Peninsula.

The objectives of the present study was to compile a database of formal and informal distribution records of Black Bass in South Africa to determine the current spatial distribution of different Black Bass species in South Africa; identify environmental variables that influence their distribution; and predict areas that are suitable but from which distribution data are unavailable to provide the first estimate of potential "invasion debt" and prioritise future survey effort. Consequently, we hypothesised that: (1) informal information sources would significantly increase the known extent of occurrence of Black Bass in South Africa; (2) the distribution of all the three Black Bass species by similar environmental factors; and (3) that Black Bass distributions would be strongly associated with human population density.

Methods

Current distribution

Formal and informal information sources were used to compile a database of occurrence records of all Black Bass species in South Africa (see Supplementary Table I). Formal distribution records housed at the South African Institute for Aquatic Biodiversity (SAIAB, unpublished data), Ezemvelo KwaZulu-Natal Wildlife (EKZN Wildlife, unpublished data), Mpumalanga Tourism and Parks Agency (MTPA, unpublished data) and the Cape Fold Ecoregion (CFE) (Dallas et al. 2017; CapeNature unpublished data) were used. These were supplemented with data from reviews by De Moor and Bruton (1988) and Ellender and Weyl (2014). To incorporate data that may have been omitted by these two reviews, an exhaustive literature search focusing on recent peer-reviewed publications (2005–2016) dealing with any aspect of the Blackburn et al. (2011) unified framework for biological invasions (transport, introduction, establishment and spread) or documenting any ecological impacts of Black Bass species in South Africa was performed.

The informal information database was compiled from an extensive search for Black Bass records in social network websites (e.g. Facebook), blog sites dedicated specifically to anglers (e.g. www.sabaa.co.za, www.bigbass.co.za), angling magazines (e.g. The Bass Angler, SA BASS) and from angling tournament records. A Boolean search using AND, OR and NOT as Boolean operators was performed between March and November 2016 using a combination of both common and scientific names for Largemouth Bass, Smallmouth Bass and Spotted Bass. All records were restricted to South Africa. Since informal data are subject to misidentification of species, data were only included in the database if the record included a photograph of the species; where capture locality could be ascertained (either via available geographic coordinates or by inference to a recognisable geographic feature). Native-range distribution records for the three Black Bass species were obtained from the Global Biodiversity Information Facility (http://data.gbif.org). The native range of each of the three species were limited to geographic areas as described in Robbins and MacCrimmon (1974) and Near et al. (2003). For each of these taxa, locality records were examined and, where multiple records were available for a single locality, only one was retained for further analysis.

Species distribution modelling

To fit the SDM (Stockwell and Peterson 2002; Phillips et al. 2006), we used distribution data from the native range in North America and complemented these with data from all countries where the three Black Bass species have established (http://data.gbif.org) and our contemporary South African dataset. To compensate for the lack of accurate and readily available environmental data on water quality variables for the application of niche models in aquatic systems, atmospheric variables are commonly used as proxies in studies on freshwater fishes (see Iguchi et al. 2004; Lübcker et al. 2014; Zengeya et al. 2015; Bae et al. 2018). The environmental variables used for this study were the 19 bioclimatic variables representing annual and seasonal climatic trends (e.g. mean temperature and precipitation) and extreme or limiting environmental variables (e.g. precipitation of the driest and wettest quarter) extracted from the WorldClim version 2.0 at 30 arc-second resolutions (Hijmans et al. 2005). Further, topographic and hydrological data (elevation, slope, topographic index and flow accumulation) and anthropogenic disturbance data (agricultural land and human population density) were also included for development of the SDM which was performed using the maximum entropy algorithm that was implemented in MAXENT (version 3.4.0) (Phillips et al. 2006). The predictive ability of ecological niche models is sensitive to the selection of environmental variables utilised to train the models and various procedures have been suggested to pre-select variables (Peterson and Nakazawa 2008; Merow et al. 2013; Zengeya et al. 2013). This study took advantage of the inbuilt method of regularisation in MAXENT that deals with the selection of environmental variables (regulating some to zero) which has been shown to perform well and is thought to out-perform other pre-selection procedures (Elith et al. 2011; Merow et al. 2013).

Models were trained using occurrence records from both native and introduced ranges (Broennimann et al. 2007; Broennimann and Guisan 2008). Since the majority of locality records were from North America, the database was spatially rarefied at 1°, 2°, 3°, 4° and 5° using the SDMtoolbox (Brown 2014) to obtain a better estimate of the species fundamental niche (Broennimann and Guisan 2008; Zengeya et al. 2013) and improve predictions of the potential future spread of the species, i.e. invasion debt (Essl et al. 2011; Rouget et al. 2016). The best performing model at which no spatial auto correlation occurred was at 1°.

As the extent of the spatial background can have a significant effect on the performance of the models (VanDerWal et al. 2009), the background was limited to hydrological basins with known species occurrence points following the recommendation by Zengeya et al. (2015). For each species, this was achieved by overlaying hydrological basins with occurrence points from both native and introduced ranges using ArcGIS® 10.4 (ArcGIS™; ESRI®, Redlands, CA) and a basin formed part of the background if it contained an occurrence point. For each of the three

Black Bass species models, the environmental variables were evaluated using correlation analysis to exclude those variables that were highly correlated ($r > 0.8$) (Dormann et al. 2013). For each pair of correlated variables, one variable was retained based its biological significance to the species (Supplementary Table II, III and IV; Clugston 1964; Bevelhimer and Breck 2009). The spatial resolution of all environmental variables was 30 arc seconds.

For each species, models were calibrated with 10,000 pseudo-absence points drawn at random from the species defined background (Phillips et al. 2006; Phillips and Dudík 2008). Occurrence records were randomly partitioned into equal sets (50%) for calibration and validation in MAXENT (Boyce et al. 2002; Phillips et al. 2006). The average performance of the model was obtained by repeating the process for ten iterations for each species. The final distribution map was created as an average of the ten projections. Models were optimised using the following parameters: regularisation multiplier of 1, random test percentage = 50, maximum iterations = 500, convergence threshold = 0.00001, only hinge features were selected and output format was set to logistic. The logistic output indicates the probability of a species presence at a default prevalence of 0.5 (Elith et al. 2011; Merow et al. 2013). Values range from 0, indicating a low probability, to 1, indicating a high probability of a species presence in a given area.

Model evaluation

All model performances were assessed using the area under the receiver operator curve (AUC), which measures the discrimination ability (between presence and background) of the models where values ≤ 0.5 indicate random predictions and values between 0.9 and 1.0 indicate acceptable predictions (Swets 1988). Although the AUC statistic has been widely used to validate niche models (Phillips et al. 2006; Elith et al. 2011), it is not necessarily an appropriate measure for presence-only model evaluation (Boyce et al. 2002; Lobo et al. 2008). As a result, model performance was further assessed using the Continuous Boyce Index (CBI) (Boyce et al. 2002; Hirzel et al. 2006). The Boyce index evaluates the ability of habitat suitability models to predict species presence in a given area (Boyce et al. 2002). This is achieved by partitioning the habitat suitability scores from each model outputs into a number of i classes of equal intervals (Boyce et al. 2002). For each class, the predicted and expected frequencies are calculated. The Predicted Frequency is the number of occurrence points predicted by the model falling into the class i divided by the total number of occurrence points used to build the model. The Expected Frequency is the number of grid cells included in class i, divided by the total number of grid cells in the whole study area. A predicted-to-expected (P/E) ratio is then calculated for each class and a Spearman rank correlation is used to evaluate if the ratio significantly increases as suitability increases (Hirzel et al. 2006). The P/E ratio values may range from -1 to 1, with negative values indicating models that predict worse than random and the positive values indicating models that are consistent with presence distribution in the evaluation dataset (Boyce et al. 2002; Hirzel et al. 2006).

Invasion debt

Invasion debt is broadly defined as the potential increase in the biological invasions that a given region will face over a particular time frame in the absence of any strategic interventions (Rouget et al. 2016). This study examined area-based invasion debt, also known as spread debt, to determine which areas are potentially suitable for invasion by any of the Black Bass species under consideration but for which no distribution records exist. This area-based invasion debt is determined by: (1) the probability that a species will become invasive, (2) the environmental suitability of a region for a species, and (3) the rate of spread (both natural and human-mediated) of that species (Rouget et al. 2016).

The probability that a species will become invasive was assigned using a deductive qualitative threshold based on the current distribution of each of the three species in South Africa. Department of Water Affairs (DWAF) quaternary catchments were used as sampling units because of the coarse scale of the occurrence records. A quaternary catchment constitutes the lowest and most detailed level in a hierarchical system of catchment management in South Africa (Midgeley et al. 1994). There are 1 947 quaternary catchments that are further aggregated into 22 Water Management Areas (WMA). A river profile with known occurrence of Black Bass was extracted from each quaternary catchment, and a value of 1 was given to river sections with known occurrence, and 0 if the river section did not contain any of the Black Bass species.

Environmental suitability for each of the three Black Bass species was delineated based on the logistic output from the MAXENT models. Areas with a probability above 0.5 were taken as suitable and those below were taken as not suitable. The area (km^2) that was predicted as suitable and occupancy (known occurrence record) was then quantified using ArcGIS® 10.4 (ArcGIS™; ESRI®, Redlands, CA). To provide a first estimate of the rate of spread, the total area of establishment based on occurrence records (excluding stocking data) was regressed against 20-year time-frames as suggested by Rouget et al. (2016). While these data infer spread, they are confounded by a lack of knowledge on sampling effort. As a result, the rate of spread needs to be recognised as a minimum estimate, and invasion debt in the context of this paper is either a true absence or a sampling deficiency. It is included here as it is valuable for directing future survey effort.

Results

The total database comprised 607 locality records for Black Bass in South Africa (see Supplementary Table I). Of these locality records, 467 (77%) originated from formal information sources and 140 (23%) from informal information sources (Supplementary Table I). The majority (82%) of records from formal information sources were from riverine environments and only 18% originated from lacustrine environments (Table 1). On the contrary, only 5% of the records from informal information sources originated from riverine environments and 95% of the records were from lacustrine environments (Table 1). Largemouth Bass were reported from 379 localities, Smallmouth Bass from 146 localities and Spotted Bass from 82 localities (Fig. 1a–c).

Informal information sources contributed 30% of Largemouth Bass, 15% of Smallmouth Bass and 8% of Spotted Bass records. Largemouth Bass was the most widespread species, recorded in 21 of the 22 WMAs. The exception was the Buffels WMA, an exclusively ephemeral system without any standing water or native fish. Smallmouth Bass and Spotted Bass were less widespread with occurrence records from 17 to 14 WMAs respectively (Table 1). The largest number of locality records were from the Olifants West WMA (102 localities) which is a conservation priority area (Ellender et al. 2017) and has been the focus of directed research on Black Bass impacts (e.g. Woodford et al. 2005; Shelton et al. 2008; Van der Walt et al. 2016). The smallest number of localities (4) were recorded from the Orange WMA (Supplementary Table I). The spread and occupancy per WMA for all three Black Bass species is presented in Fig. 1.

Largemouth Bass

For Largemouth Bass, model performance was good (AUC = 0.86; CBI = $p < 0.001$) and the variables contributing most to the model performance were flow accumulation (26.4%), isothermality (height of the day-to-night temperature oscillation relative to the summer-to-winter (annual) oscillations) (25.3%), precipitation of coldest quarter (16.3%), population density (6.4%) and precipitation seasonality (6%) (Table 2). Areas that were predicted as highly suitable were mainly associated with maximum temperatures of warmest month between 19 and 30 °C (optimum 26–27.5 °C), high flow accumulation and population densities (Supplementary Fig. 2). The jack-knife analysis on training and test gain and AUC test data showed that the environmental variable with the highest gain when used in isolation was flow accumulation and the environmental variable that decreased the gain the most when it was omitted was flow accumulation. As a result, the areas that were predicted as most suitable (> 0.5) for Largemouth Bass were in coastal areas from the Berg WMA in the CFE and extending up to the Mfolozi WMA in KwaZulu-Natal (Fig. 2a). Inland, sections of the Komati and Olifants North WMA were also predicted as highly suitable (Fig. 2a).

The total area predicted as suitable for Largemouth Bass was ca. 98,253 km of total river length in an extension of ca. 543,804 km^2 (Table 3). Current occupancy (rivers that were predicted as suitable and from which Largemouth Bass records are available) was ca. 27,509 km (28%) (Table 3). Subsequent invasion debt was estimated at 72%. The total length of rivers that were predicted as unsuitable were ca. 75,631 km in an area of ca. 631,463 km^2 and occupancy in this area was only at ca. 3884 km of river length indicating a 5% modelling error.

Table 1 Summary of records of Black Bass species in different water management areas of South Africa based on the occurrence records obtain from both formal and informal information sources used for this study

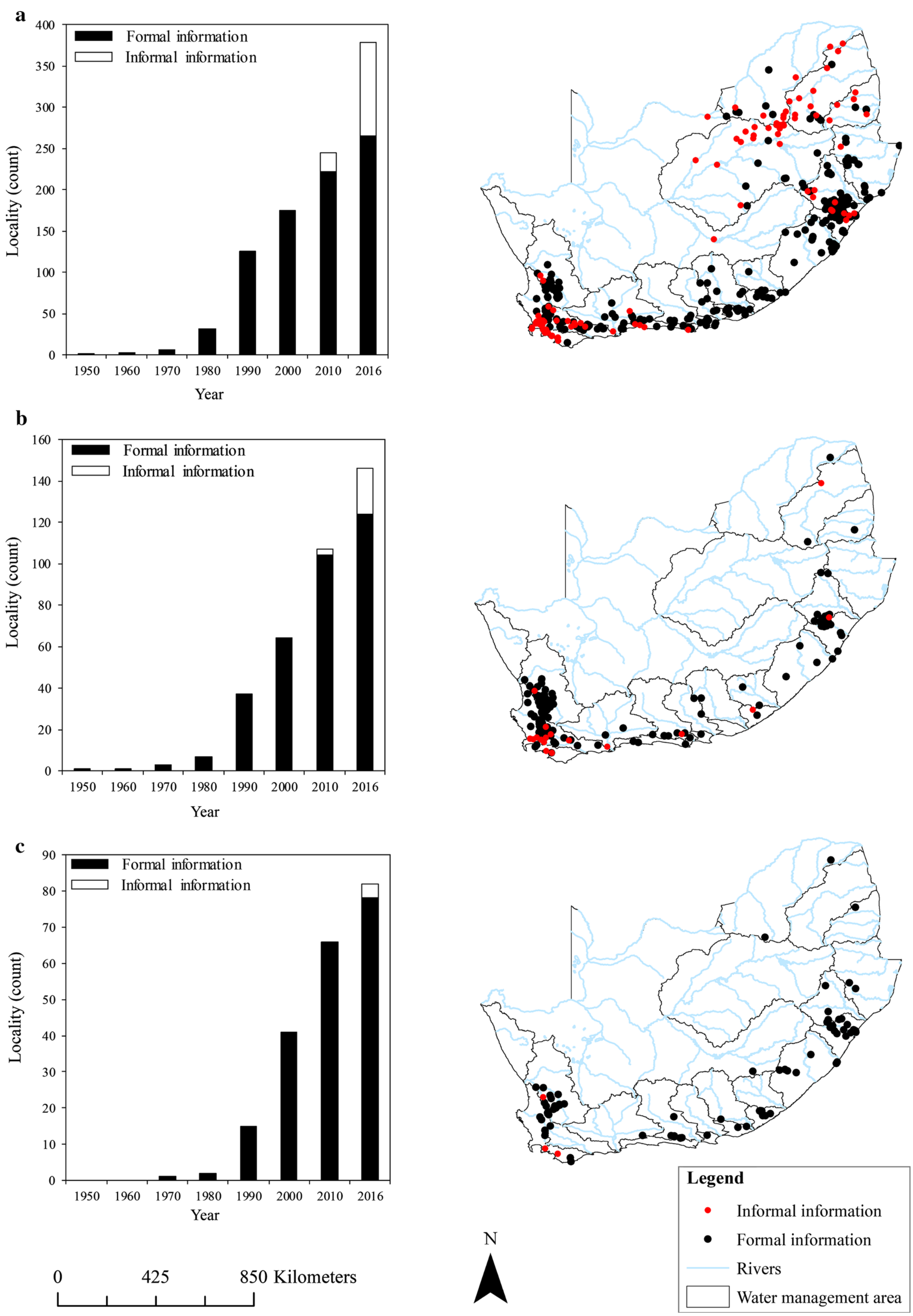
Water management area	Surface area (km^2)	River length (km)	Formal information sources			Informal information sources		
			Largemouth Bass	Smallmouth Bass	Spotted Bass	Largemouth Bass	Smallmouth Bass	Spotted Bass
A—Limpopo	97,353	12,508	4	1	2	11	0	0
B—Olifants North	65,540	10,376	6	1	0	9	1	0
C—Vaal	179,789	22,885	7	0	0	17	0	0
D—Orange	379,999	41,643	2	0	1	1	0	0
E—Olifants west	46,755	7452	33	44	19	4	1	1
F—Buffels	26,733	3342	0	0	0	0	0	0
G—Berg	2454	3761	10	20	6	40	11	2
H—Breede	15,136	2864	22	16	0	10	5	0
J—Gouritz	43,650	7668	13	1	1	1	1	0
K—Krom	704	1470	7	3	0	4	0	0
L—Gamtoos	33,414	6003	5	7	8	1	1	1
M—Swartkops	256	427	9	1	1	0	0	0
N—Sundays	20,420	3699	5	2	0	0	0	0
P—Bushmans	519	1312	15	0	0	0	0	0
Q—Great fish	28,930	5746	5	1	2	0	0	0
R—Keiskamma	764	1876	6	1	8	0	1	0
S—Kei	19,550	4670	4	2	0	0	0	0
T—Mzimvubu	44,060	10,452	23	4	7	0	0	0
U—Mkomazi	17,074	4074	50	9	15	6	1	0
V—Tugela	26,770	5380	20	10	5	4	0	0
W—Mfolozi	53,870	10,683	16	0	2	1	0	0
X—Komati	27,960	5585	3	1	1	5	0	0
Total	1,129,246	163,500	265	124	78	114	22	4

See supplementary Table 1 for informal source details

Smallmouth Bass

The Smallmouth Bass model performance was good (AUC = 0.87; CBI = $p < 0.001$) and the variables contributing most to the model performance were precipitation of warmest quarter (28.6%), flow accumulation (26%), topographic index (12.9%) and precipitation of coldest quarter (10.3%) (Table 2). The response curves showed that the areas that were predicted as highly suitable for Smallmouth Bass were mainly associated with mean temperature of warmest quarter (range = 19–25 °C, optimum 21–24 °C) and precipitation of the coldest quarter (optimum > 600 mm) (Supplementary Fig. 3). The jack-knife analysis on training and test gain and AUC test data showed that the environmental variable with the highest gain when used in isolation was precipitation of warmest quarter (> 100 mm) and the environmental variable that decreased the gain the most when it was omitted was topographic index. As a result, the areas that were predicted suitable (> 0.5) for Smallmouth Bass occurrence were river basins in the CFE (Fig. 2b).

The areas predicted as suitable for Smallmouth Bass was estimated at ca. 79,976 km of total river length in an extension of ca. 461,163 km^2 (Table 3). Currently, occupancy of Smallmouth Bass was only at total river length of ca. 6356 km (7.9%) and the invasion debt was 92.1%. The area predicted unsuitable was 93,902 km in an area of ca. 713,637 km^2 with an occupancy of less than 1% of the total area (Table 3).


a
Formal information
Informal information
Locality (count)
400
350
300
250
200
150
100
50
0
1950
1960
1970
1980
1990
2000
2010
2016
Year
b
Formal information
Informal information
Locality (count)
160
140
120
100
80
60
40
20
0
1950
1960
1970
1980
1990
2000
2010
2016
Year
c
Formal information
Informal information
Locality (count)
90
80
70
60
50
40
30
20
10
0
1950
1960
1970
1980
1990
2000
2010
2016
Year
0
425
850 Kilometers
N
Legend
Informal information
Formal information
Rivers
Water management area

◀**Fig. 1** The detection rate of the three Black Bass species in South Africa projected from different information sources, **a** Largemouth Bass, **b** Smallmouth Bass and **c** Spotted Bass

Spotted Bass

The model was good (AUC = 0.88; CBI = $p < 0.001$) and the variables that contributed most to model performance were flow accumulation (27.5%), topographic index (18.9%), agricultural land use, annual mean temperature (11.4%) and precipitation of coldest quarter (10.6%) (Table 2). The response curves showed that the areas that were predicted as highly suitable for the establishment of Spotted Bass were mainly associated with the mean temperature of the driest quarter (range = 20–28 °C, optimum = 23–26 °C) and flow accumulation (Supplementary Fig. 4). The jack-knife analysis on training and test gain and AUC test data showed that the environmental variable with the highest gain when used in isolation (most useful information by itself) was topographic index and the environmental variable that decreased the gain the most when it was omitted was topographic index. The areas that were predicted as suitable (> 0.5) for Spotted Bass were located along the coastal areas of South Africa from the Berg WMA and extending up to the Mfolozi WMA in KwaZulu-Natal (Fig. 2c).

The area predicted as suitable for Spotted Bass spotted was estimated at 18,404 km of total length in river systems in an extension of ca. 85,976 km^2 (Table 3). Current occupancy in the suitable area was estimated at 4347 km of the rivers 23.6% and the invasion debt was 76.4%. Spotted Bass was only recorded in < 1% of the areas that were predicted as unsuitable 1086 km of the rivers in ca. 1,081,612 km^2 of the total area (Table 3).

Discussion

Black Bass distributions

This study demonstrated that, with appropriate data quality control measures, informal information sources were a useful tool for extending the knowledge of the occurrence of Black Bass from relatively well studied riverine environments to poorly studied lacustrine environments. From our current dataset, it was after 2010 that most records of Black Bass were publicised online, predominantly in anglers' social media and blog platforms. The increase of Black Bass records in informal sources can be attributed mainly to

Table 2 Environmental variables and the relative contribution (%) of each variable used to predict the potential spread of Largemouth Bass, Smallmouth Bass, Spotted Bass and Florida Bass in South Africa

Environmental variable	Largemouth Bass	Smallmouth Bass	Spotted Bass
Annual mean temperature	–	–	**11.4**
Isothermality	**25.3**	2.7	–
Temperature seasonality	–	–	1.6
Temperature annual range	–	–	2.4
Mean temperature of wettest quarter	2.2	1	–
Mean temperature of driest quarter	–	–	1.6
Mean temperature of warmest quarter	–	1.4	–
Annual precipitation	1.5	–	–
Precipitation of driest month	2.9	–	1.7
Precipitation seasonality	6	2.9	–
Precipitation of warmest quarter	4.1	**28.6**	4
Precipitation of coldest quarter	**16.3**	**10.3**	**10.6**
Flow accumulation	**26.4**	**26**	**27.5**
Population density	**6.4**	2.1	1
Agricultural land	2.4	**8.3**	**18.2**
Topographic index	1.9	**12.9**	**18.9**
Slope	1.2	0	0
Elevation	1	0	0

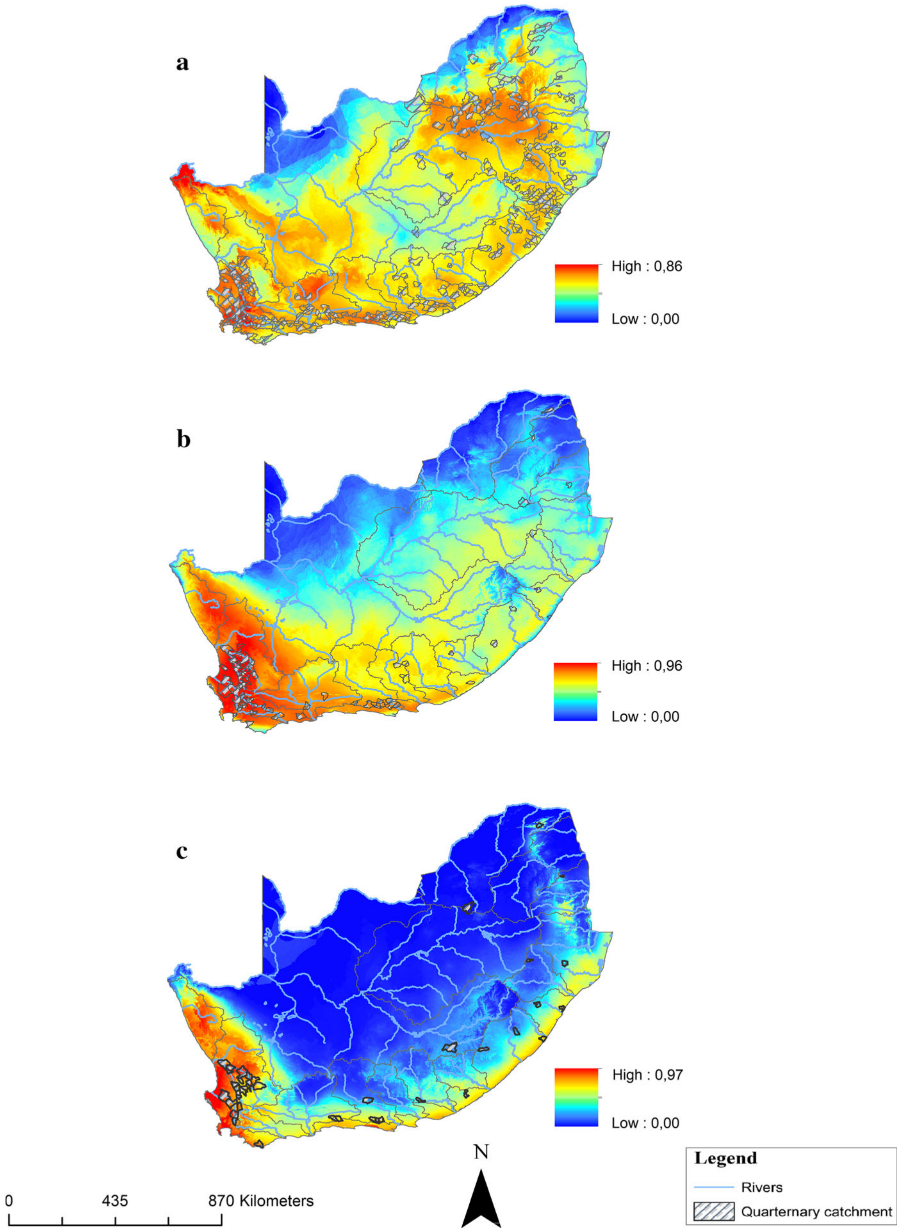


Fig. 2 The predicted distribution of the three Black Bass species in South Africa and the quaternary catchments with known Black Bass occurrence, **a** Largemouth Bass, **b** Smallmouth Bass and **c** Spotted Bass

the launch of Facebook in 2004 which facilitated the sharing and access to angler catch records (Gago et al. 2016). By incorporation informal information sources into our dataset we increased the number of known localities by 30%, thereby supporting our first hypothesis that informal data sources would significantly increase the known extent of occurrence of Black Bass.

As inland fisheries were, until recently, not a priority for South Africa (Weyl et al. 2007), most formal fish surveys in South Africa were conducted with a conservation focus (e.g. van der Walt et al. 2016). This disparity is explained by most lentic environments in the country being impoundments that are generally considered of low conservation importance (Beatty et al. 2017) but are used extensively for angling (Hargrove et al. 2015). As a result, the current study highlights the value of combining both formal and informal information sources to provide a broader representation of the extent of occurrence of Black

Table 3 Summary of the total river length and current occupancy of Black Bass species at different rivers per water management area of South Africa

Water management area	Surface area (km^2)	River length (km)	Suitable river length (km)			Current occupancy (km)		
			Largemouth Bass	Smallmouth Bass	Spotted Bass	Largemouth Bass	Smallmouth Bass	Spotted Bass
A—Limpopo	97,353	12,508	4191	0	0	1945	130	237
B—Olifants North	65,540	10,376	4947	0	0	1641	248	0
C—Vaal	179,789	22,885	13,975	10,009	0	3025	0	0
D—Orange	379,999	41,643	14,198	17,314	392	722	0	237
E—Olifants West	46,755	7452	3385	7452	4684	1584	1756	1561
F—Buffels	26,733	3342	2438	3284	2595	0	0	0
G—Berg	2454	3761	2740	2951	3191	2061	1318	837
H—Breede	15,136	2864	2864	2864	748	1725	890	27
J—Gouritz	43,650	7668	7204	7668	152	1120	162	173
K—Krom	704	1470	1470	1261	1470	450	0	0
L—Gamtoos	33,414	6003	5238	6003	622	864	777	378
M—Swartkops	256	427	427	427	24	316	0	0
N—Sundays	20,420	3699	3395	3699	261	532	261	0
P—Bushmans	519	1312	1312	1312	812	827	0	0
Q—Great Fish	28,930	5746	3852	5746	0	743	129	90
R—Keiskamma	764	1876	1876	1867	923	745	65	146
S—Kei	19,550	4670	1712	2420	147	370	79	0
T—Mzimvubu	44,060	10,452	6901	4591	2077	2307	246	276
U—Mkomazi	17,074	4074	3265	1092	306	2611	153	235
V—Tugela	26,770	5380	5380	16	0	1750	94	38
W—Mfolozi	53,870	10,683	5256	0	0	1555	0	81
X—Komati	27,960	5585	2227	0	0	616	48	31
Total	1,129,246	163,500	98,253	79,976	18,404	27,509	6356	4347

Bass in South Africa. This is important because the three species have different habitat preferences which affect the probability that they are detected in lentic and lotic environments. Van der Walt et al. (2016) in a survey of 42 tributary streams of the Olifants–Doring River System, for example, showed that Smallmouth Bass and Spotted Bass co-occurred in most sections of rivers, inhabiting the fast-flowing riffles and pools, while Largemouth Bass were restricted to slow-moving headwater stream and adjacent ponds. This highlights the importance of the inclusion of data from both lotic and lentic environments in distributions.

From the analysis of spread/detection rate, it is also evident that detections have increased with increasing survey effort since the 1980s and the inclusion of informal data (see Fig. 1). This can be attributed to recent efforts by government and conservation entities to document the spread of non-native species (Ellender and Weyl 2014), and the increased use of online platforms by anglers which facilitates the mining of informal data. The current dataset is the most complete set of distribution records for Black Bass in South Africa and was the basis for our subsequent model of the potential spread of the three Black Bass species in South Africa.

Species distribution modelling

Model outputs closely followed the know distributions of the three species (Fig. 2a–c) but only partly supported our second hypothesis that the distribution of all the three Black Bass species was determined by similar environmental factors. While flow accumulation, a variable showing association to mainstream rivers and impoundments, was an equally important variable for all three species, the importance of other environmental variable differed between species. In overcoming the establishment barrier for invasions (Blackburn et al. 2011) climate matching the native is often a significant factor in the establishment (Marr et al. 2010). Inter-specific differences in the environmental drivers therefore need to be viewed in the context of the habitat preferences and requirements of the three species under consideration.

The model outputs for Largemouth Bass indicated that most of the country was environmentally suitable (Fig. 2a). In terms of environment, the response curves show that Largemouth Bass were likely to occur in warmer areas where maximum temperatures ranges between 19 and 30 °C. This was expected as temperature is known to be positively related to growth, spawning and the survival of eggs and embryos (Clugston 1964; Beamish et al. 2005). Our findings are congruent with Bae et al. (2018) who found temperature to be the most important predictor of Largemouth Bass distributions. The preference of Largemouth Bass for slow flowing and lentic environments (Jackson 2002; Claussen 2015) was demonstrated by their high association with flow accumulation. As a result, the presence of more than 3000 impoundments spread across South Africa (Weyl et al. 2007) is likely to facilitate Black Bass invasions as has been demonstrated for this and other invasive species elsewhere (Johnson et al. 2008; Bae et al. 2018).

For Smallmouth Bass, the SDM showed that areas most suitable for Smallmouth Bass were associated with the Mediterranean climate region in the CFE with high summer temperatures and high precipitation during the coldest quarter. This fits well within the high maximum temperature tolerance (34.8 °C) and thermal optima for spawning and growth (12.1–21 °C) for this species (Beitinger et al. 2000; Brewer and Orth 2014).

For Spotted Bass, the area that were predicted to be suitable are located between the coast and the escarpment of South Africa up to mid KwaZulu-Natal. The most significant climatic variables identified by the Spotted Bass models were annual mean temperature and precipitation of coldest quarter. Unlike Largemouth Bass and Smallmouth Bass, spawning of Spotted Bass is not stimulated by rising water levels following precipitation (Sammons et al. 1999; Beamish et al. 2005). However, suitable temperatures between 14 and 23 °C are required for successful spawning (Churchill and Bettoli 2015). The significance of temperature was also observed in the response curves where habitat suitable for Spotted Bass was associated with the mean temperature of the driest quarter with a range of 20–28 °C, which was congruent with the requirements for successful spawning for Spotted Bass (Sammons et al. 1999).

Human activity

Our third hypothesis, that because Black Bass are actively introduced to develop opportunities for angling, Black Bass distributions would be strongly associated with human population density, was not supported by the analyses. Population density explained only 6.4% of the distribution of Largemouth Bass, 2% for Smallmouth Bass and 1% for Spotted Bass. This was surprising because Black Bass are popular among anglers, whom have been shown to be a major vector for their spread in South Africa (e.g. De Moor 1996; Ellender et al. 2014; Weyl et al. 2017) and elsewhere (Jackson 2002; Long et al. 2015). The lack of direct association with human population density is likely to be a result of the wide spread stocking by government agencies and recreational angling societies soon after the introduction of these species (Ellender et al. 2014). Ellender et al. (2014) describes how the hatchery infrastructure and distribution and stocking network developed for trout in the early 1900s was used to introduce Black Bass into parts of almost every major river system in South Africa by 1940. As these government subsidised stocking events were likely informed by the presence of suitable habitat rather than by human population density, the current extent of occurrence of Black Bass populations is only weakly correlated with human population density. The relatively higher association of Smallmouth Bass and Spotted Bass with agricultural land

(8–18%) in comparison with Largemouth Bass (1.9%) is likely to be an artefact of their higher occurrence in the CFE where most low lying areas are agricultural land.

Invasion debt and survey priorities

Non-native invasions may be characterised by a substantial lag phase from the time of introduction, subsequent establishment and spread in the novel environments (Essl et al. 2011; Rouget et al. 2016). These delays are mainly influenced by propagule pressure (Simberloff 2009) and the conditions in the novel environments, i.e. competition (De Moor 1996; Jackson et al. 2017) and climate (Jackson and Sax 2009). The results of this study suggest that there is a considerable area-based invasion debt for Largemouth Bass and Smallmouth Bass. For Largemouth Bass, there is an extensive area based invasion debt across all WMAs. Similarly, besides having lesser areas that are suitable when compared to Largemouth Bass, Smallmouth Bass also have an extensive area that remains unoccupied. Further, we also find overlaps in rivers that are predicted as suitable for both Black Bass species specifically in the CFE and the Vaal WMA. Although these are based on crude estimates and limited by sampling effort, it is concerning given the popularity of the species among anglers, therefore increasing the possibility of their translocation into new areas (Hargrove et al. 2015; Long et al. 2015; Weyl et al. 2015).

Conservation implications

The global spread of Black Bass species has been driven by the desire to create recreational angling opportunities (Jackson 2002; Long et al. 2015), and in some areas, including South Africa, there is still paucity of information relating to the ongoing introduction and spread of the *Micropterus* species (Ellender et al. 2014; Hargrove et al. 2015, 2017; Weyl et al. 2017). This is a problem because Black Bass exert considerable predation pressure on the biota in invaded environments. In South Africa, this has resulted in the extirpation and fragmentation of native fish communities (Ellender and Weyl 2014; Kimberg et al. 2014; Ellender et al. 2018). Of particular concern is the CFE which contains 42 native fish taxa, most of which are endemic and IUCN red-list evaluated as Endangered (Ellender et al. 2017). As all three Black Bass species already occur in the CFE and environmental conditions in this area are highly suitable for them, actions limiting their spread is critical to prevent further impacts on an already imperilled native fish fauna (Ellender et al. 2017).

Limiting the spread and impact of Black Bass in South Africa requires accurate contemporary information on their current distribution. While the current approach of using informal information sources enhanced our understanding of Black Bass distributions, additional survey data will be necessary to implement national legislation attempting to limit the spread of Black Bass into areas that are not already invaded (see Woodford et al. 2017). As this will require considerable resources to implement, we suggest that such surveys initially focus on the "invasion debt" areas identified in this study.

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